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# SALT AND WATER BALANCE IN TWO MARINE SPIDER CRABS, *LIBINIA EMARGINATA* AND *PUGETTIA PRODUCTA*. II. APPARENT WATER PERMEABILITY

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In studies of salt and water balance, permeability is an important parameter since knowledge of it, together with a knowledge of the appropriate driving force, permits predictive statements concerning net fluxes. A complication in this matter is that permeability may vary. A reduction in tracer water exchange rate has been found in a number of osmoregulating decapod crustaceans transferred to a dilute medium (*Rithropanopeus harrisii,* Smith, 1967; Capen, 1972: *Carcinus maenas,* Smith, 1970; Berlind and Kamemoto, 1977: *Hemigrapsus nudus,* Smith and Rudy, 1972; *Palaemonetes pugio,* Roseijadi, Anderson, Petrocelli and Giam, 1976). However, not all osmoregulating decapods respond to a dilute salinity in this fashion (*Palaemonetes varians,* Parry, 1955: *Carcinus maenas,* Rudy, 1967: *Penaeus duorarum* and *Uca* spp., Hannan and Evans, 1973), nor does the same species necessarily respond in the same way under similar conditions. Also, there are alternative explanations for changes in water exchange other than a true change in permeability (Smith, 1970, 1976). However, the adaptive value of a reduction in water permeability when the osmotic gradient is increased is quite clear and, on the basis of the available evidence, a strong argument can be made in favor of changes in water permeability.

There is, perhaps, little reason to predict that an osmoconforming crab would respond to dilute salinity with a reduction in permeability; however, when specimens of *Libinia emarginata* were transferred from 100 to 80% sea water, there was a reduction of 30% in water exchange after the first hour (Cornell, 1973). It can be argued that a reduction in water permeability is also an adaptive response to dilute salinity in an osmoconformer, but the argument is open to question. In the present study, some aspects of apparent water permeability have been examined in the osmoconforming crabs *Libinia emarginata* and *Pugettia producta* and in the osmoregulating crab *Carcinus maenas.* An attempt is made to identify some factors which may be important in changes in water exchange rates.

## MATERIALS AND METHODS

### *General procedures*

Specimens of *Pugettia producta* were maintained at 10–12° C in filtered sea water (SW), about one crab per 4 liters, at the University of California, Berkeley, California. Specimens of *Carcinus maenas* and *Libinia emarginata* were maintained at 19 to 21° C in running SW at the Marine Biological Laboratory, Woods

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Hole, Massachusetts. The SW used at Berkeley was obtained from the Bodega Marine Laboratory, Bodega Bay, California and had an osmotic pressure of about 1015 milliosmols, while that at Woods Hole was about 945 milliosmols.

Exchange rates of tracer water were measured using $D_2O$ according to the technique described by Welsh, Smith and Kammer (1968). Specimens of *Carcinus* and *Libinia* were immersed for 11 and 15 min, respectively, in aerated 3-liter solutions of sea water (SW) plus 2.0 to 2.5% $D_2O$ maintained at constant temperature ($21 \pm 0.5°$ C) in a bath of running SW. Samples of blood were withdrawn by puncturing an arthrodial membrane with a drawn-out Pasteur pipet.

Heart rate was determined by implanting chronic platinum electrodes which just penetrated the hypodermis over the region of the heart. The electrodes were cemented to the carapace with quick-setting ("five-minute") epoxy glue, after scraping away the epicuticle from the region where the bond was to be made. Electrodes were implanted at least 24 hr prior to an experiment.

Measurements of pressure changes caused by the beat of the scaphognathite were made with a Statham model P23BC pressure transducer connected by polyethylene tubing (P.E. 190, 0.047 inch = 1.2 mm inside diameter) to the cut-off tip of an 18-gauge hypodermic needle. A hole, positioned by external landmarks, was drilled through the carapace, and the needle tip was inserted through the hole and into the branchial chamber, just posterior to the scaphognathite. The needle tip was cemented in place with quick-setting epoxy. Measurements of heart and scaphognathite rates were recorded on a Grass Instrument Co. model 7a polygraph.

Isolated gills from *Libinia* were first flushed and then perfused with a solution containing inorganic ions in ratios given for *Cancer* perfusion fluid (Welsh, Smith and Kammer, 1968) and dextrose (1.5 mM). The solution was buffered to pH 7.2 with "Tris" (about 25 mM) and the final solution was adjusted to 945 milliosmols. A peristaltic pump, either a Buchler Instruments Polystatic Pump or a Sage model 375A, controlled the rate of perfusion and recirculated fluid between the gill and a small reservoir from which samples were taken. The total fluid volume of the system was about 1.5 to 2.0 ml. Polyethelene tubing was fitted to the afferent and efferent vessels and secured with silk thread. A small clamp, placed about 5 mm from where the tubing entered the gill, maintained the proper spatial relationship between the two tubes. A rod, attached to the clamp, suspended the preparation in a beaker containing 300 ml of aerated SW plus 3% $D_2O$ maintained at $20 \pm 0.1°$ C. Constant stirring was provided by a magnetic stirrer.

### *A practical approach to estimates of apparent water permeability*

Two different measurements of water permeability can be made, osmotic permeability and diffusive permeability.

Osmotic water permeability $(P_{osm}) = L_pRT/\bar{V}_w$, where $L_p$ is the hydraulic conductivity, R is the gas constant, T is the absolute temperature, and $\bar{V}_w$ is the partial molar volume of water. $L_p$ is a measurement of permeability and, simply stated, is a flux divided by a driving force. The advantage of converting $L_p$ into $P_{osm}$ is that by doing so, it is possible to compare $P_{osm}$ with estimates of diffusive water permeability, since both can be expressed in the same units.

Unfortunately, the conditions under which $L_p$ may be determined are incompatible with most whole-animal experiments. However, the concept of expressing a net flux divided by a driving force is useful and has been adopted here. The symbol $L_p{}^*$ will be used to indicate a net flux divided by osmotic pressure and values will be expressed in $\mu l/(g \cdot hr \cdot osmol)$. $P_{osm}{}^*$ will be expressed in $cm^3/(g \cdot sec)$ in keeping with the more conventional units $[cm^3/(cm^2 \cdot sec) = cm/sec]$. When expressed in $cm^3/(g \cdot sec)$, $L_p{}^*$ is in the units of $cm^3/(g \cdot sec \cdot atm)$, $R = 82.04\ cm^3/(atm \cdot mole \cdot degree)$, T is absolute temperature in degrees K, $\bar{V}_w = 18\ cm^3/mole$. Since permeable surface area is unknown in a whole animal, weight has been substituted and allowances must be made for this factor in comparisons where large weight differences occur.

In a decapod $L_p{}^*$ will reflect not only water permeability, but other factors as well. $L_p{}^*$ only provides an adequate description of water movements across an ideal semi-permeable membrane which separates two solutions containing non-electrolytes. The characterization of a membrane which is permeable to solutes is more complex. When the solute is composed of univalent ions, the phenomenological approach based on irreversible thermodynamics requires the determination of six membrane coefficients (see review by House, 1974). Since water movement is influenced by the presence of permeant ions, $L_p$ must be measured in the absence of an osmotic gradient and current flow, and in the presence of a driving force of hydrostatic pressure. Clearly, the measurement of net water fluxes under these conditions would be difficult in an intact decapod crustacean. It is believed, despite some objections, that the present approach provides a meaningful way of dealing with the problem of making measurements of "water permeability" in a whole animal.

Diffusive water permeability $(P_d) = kv/A$, where v is the volume of the water pool, A is surface area and k is a rate constant. In a well-stirred, two-compartment system in a steady state, the tracer concentration, $f(t)$, in the very small compartment which initially contains no tracer is given by $f(t) = C(1 - \exp -kt)$, where t is time, C is the concentration in the very large compartment, and k is a rate constant. The value of k is proportional to the diffusive water permeability, and in similar animals the constant is similar, so that k should provide a reasonable basis on which to make comparisons of permeability. In the present study, the results of the experiments with tracer water will be expressed in terms of the rate constant k in (1/hr), where $k = (1/t)\ \log_e[C/(C - f(t))]$. The symbol $P_d{}^*$ in $cm^3/(g \cdot sec)$ will indicate the analog to the more familiar $P_d$ in cm/sec.

## RESULTS

### *Estimates of $L_p{}^*$*

For an animal in a steady state, $L_p{}^*$ may be estimated from the urine production rate and the osmotic difference between the blood and the medium. This approach is well suited to osmoregulators, but in an osmoconformer, the osmotic difference can be small (about 2 milliosmols in *Pugettia*) and thus subject to large errors in measurement. An alternative approach is to determine the rate of weight gain at time 0, when an animal is transferred to a dilute test medium.

TABLE I

*Estimates of* $L_p$* *in normal and nephropore-occluded specimens of* Libinia emarginata *and* Pugettia producta. *Analysis of covariance of the regressions of the transformed weights (see text) vs time indicates that there are significant differences between the initial rates of weight gain for normal specimens of* Libinia ($N = 19$) *and* Pugettia ($N = 10$) ($P < 0.001$) *and for nephropore-occluded specimens of* Libinia ($N = 7$) *and* Pugettia ($N = 7$) ($P < 0.05$).

| Animal | *Libinia* | | *Pugettia* | |
|---|---|---|---|---|
| State of nephropores | Normal | Occluded | Normal | Occluded |
| Average weight (g) | 152 | 144 | 121 | 117 |
| Rate of weight gain at $t = 0$, expressed in volume [$\mu$l/(g·hr)] | 30 | 33 | 70 | 67 |
| Osmotic gradient at $t = 0$ (osmols) | 0.189 | 0.189 | 0.203 | 0.203 |
| $L_p$* [$\mu$l/(g·hr·osmol)] | 159 | 174 | 345 | 330 |

At this moment, urine production is equal to that in the normal medium, the osmotic gradient is known, and the rate of weight change can be assumed to equal the net flux of water.

Empirically, it has been found that the equation $f(t) = Ct \exp -jt$ (where $f(t)$ is the weight at time t, C is a constant and j is a rate constant) provides a good description of weight changes in a number of decapods transferred to a dilute medium. At time 0, the rate of change of $f(t)$ can be determined from the first derivative and is simply C. Thus, by plotting the transformed weight data (transformed by $\log_e[((W_t/W_o) - 1)(1/t)]$, where t is time and $W_t$ and $W_o$ are the weights at times t and 0, respectively) against time, the y intercept can be determined, and the value of C is equal to $\text{antilog}_e$ of the y intercept. The resulting plots are seldom strictly linear, but they are sufficiently so that it is an easy task to estimate the intercept.

Using the above technique, the rates of weight gain were obtained from data on normal and nephropore-occluded animals (Cornell, 1976). Values for $L_p$* were calculated from these rates and the changes in osmotic gradients. The results, presented in Table I, suggest that *Pugettia* is about twice as permeable to water as *Libinia*. The average for normal and nephropore-occluded animals is 166 and 338 $\mu$l/(g·hr·osmol) for *Libinia* and *Pugettia*, respectively. From these estimates, it is possible to calculate the expected osmotic difference necessary to produce an influx of water equal to the rate of normal urine production (2.1 and 2.5 $\mu$l/(g·hr) for *Libinia* and *Pugettia*, respectively, Cornell, 1979); thus, $2.1/166 = 13$ milliosmols and $2.5/388 = 7.4$ milliosmols for *Libinia* and *Pugettia*, respectively. The estimate of 7.4 is greater than the observed value of 2 milliosmols in *Pugettia*. The osmotic difference between the blood and the medium is not known for *Libinia*; however, in both cases, these estimates are greater by about an order of magnitude than the colloid osmotic pressure (Mangum and Johansen, 1975). These discrepancies raise questions concerning the mechanism for the entry of water in an osmoconforming crab. One interpretation of the present results is that, whatever the mechanism, the driving force is equivalent to an osmotic pressure of between 7 and 13 milliosmols.

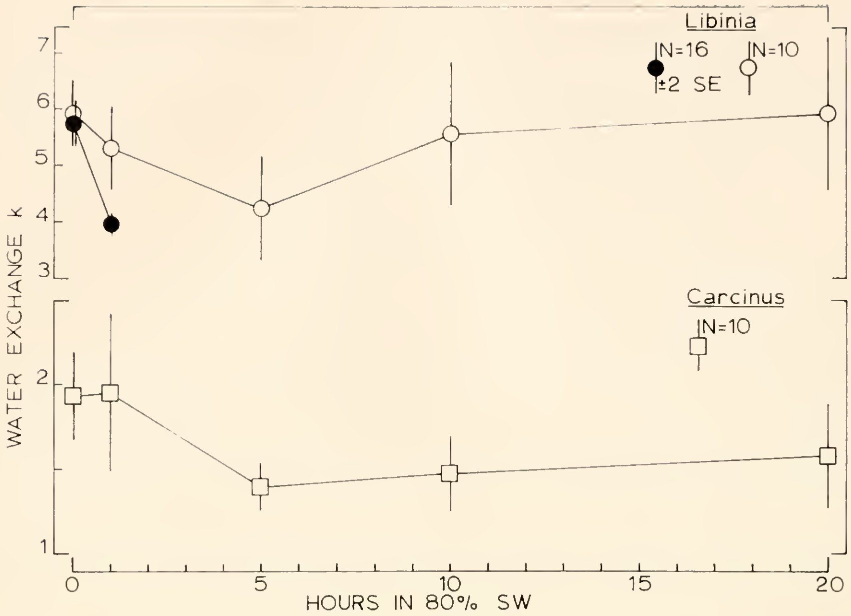

FIGURE 1. Changes in $D_2O$ water exchange rates in specimens of *Libinia emarginata* and *Carcinus maenas* transferred from 100 to 80% SW, expressed as k in (1/hr), the hourly water exchange fraction. For specimens of *Libinia*, the results from two experiments are shown: the first, is indicated by the solid circles (average weight of crabs, 168 g); the second, is indicated by the open circles (220 g). For specimens of *Carcinus*, the results are indicated by the open squares (22 g).

I have calculated $L_p$* for specimens of *Pugettia* during the first several hours after transfer to 80% SW. The calculations suggest that there is a reduction in $L_p$* of about 60% during the first hour; however, this may be an artifact. The calculations, based on measurements which have relatively large variances (weight gain, urine production, and the osmotic gradient, Cornell, 1976), become increasingly sensitive with time to errors in measurement. Since a plot of the logarithm of the osmotic gradient between the blood and the medium versus time is not significantly curvilinear, a large reduction seems unlikely. Perhaps the safest conclusion is that the data are inadequate to indicate whether or not a short-term change in $L_p$* occurs.

### *Etimates of k*

The results of two experiments in which specimens of *Libinia* were transferred from 100 to 80% SW are shown in Figure 1. For practical reasons, the points at time 0 were actually determined 24 hr prior to the transfer of animals to 80% SW. In the first experiment, k in (1/hr) was 5.68 for animals in SW and 3.99 for the same group after one hour in 80% SW, a reduction of 30% ($P < 0.001$, paired *t*-test). The second experiment is similar to the first, but was carried out for a longer period of time. In this experiment, k, measured after one hour of

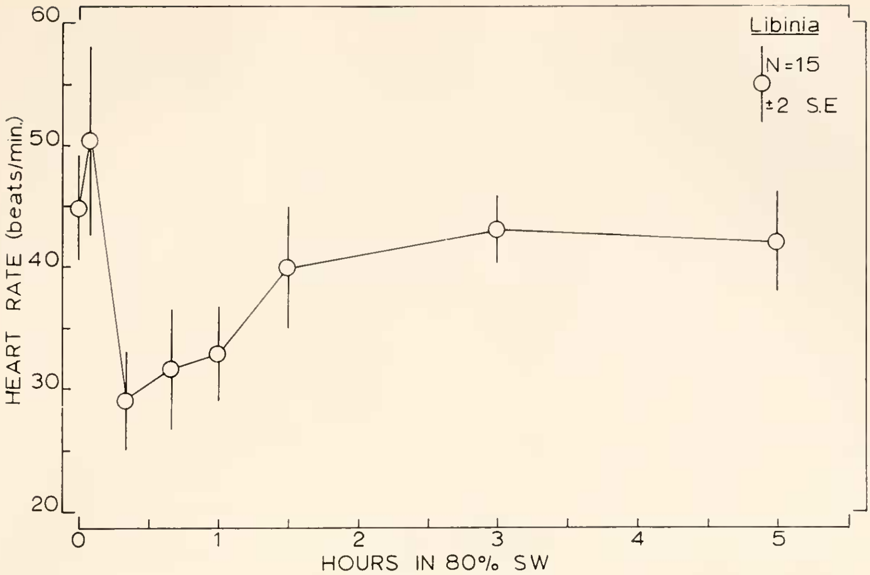

FIGURE 2. Changes in heart rate of specimens of *Libinia emarginata* transferred from 100 to 80% SW. Rates were determined from 2-min intervals (average weight of crabs, 150 g).

exposure to 80% SW, was not significantly different from k in 100% SW, but after five hours there was a significant decrease ($P < 0.005$, paired *t*-test). The reduction in k appears to be a transient response, since k returned to normal after ten hours. The cause of the difference in k between the two groups of animals is unknown.

While the reduction in k in *Libinia*, an osmoconforming crab, appears to be a transient response, long-term reductions have been reported for a number of osmoregulating crabs transferred to dilute salinities. The time course for this change has been reported for *Rithropanopeus* (Capen, 1972). In this crab, there is a reduction in k within the first hour of transfer from 75 to 10% SW. The initial phase of this reduction is not unlike that in *Libinia*, both in the initial rate of change and in the final extent of the change. It is of some interest to know if the time course in *Rithropanopeus* is similar to that in other osmoregulating crabs that have a reduced k in dilute media. To determine this, k was measured in specimens of *Carcinus maenas* transferred from 100 to 80% SW. The results of this experiment appear in Figure 1. For specimens of *Carcinus* in 100% SW, k was 1.94. After one hour of exposure to 80% SW, there was little change in k, but after five hours of exposure, the value had decreased by about 30% ($k = 1.41$, $P < 0.005$, paired *t*-test).

In the present study, k was determined in animals which were in a steady state, and in animals which were adapting to 80% SW and were not in a steady state. Therefore, it seems appropriate to ask if the reduction in k can be attributed solely to a change in state. The answer is probably "no." Two variables will be considered, surface area and volume of the water pool. The

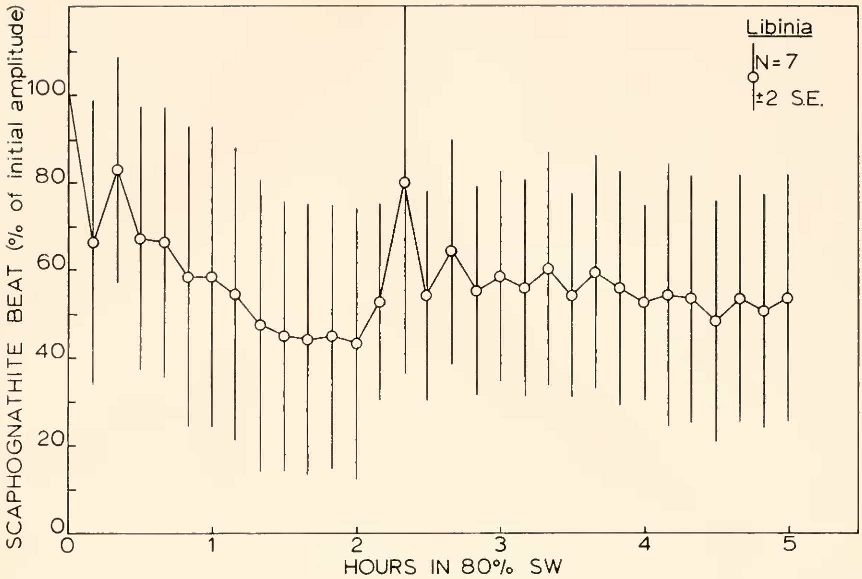

FIGURE 3. Changes in the amplitude of scaphognathite beat in specimens of *Libinia emarginata* transferred from 100 to 80% SW. Results are expressed as a percentage of the pressure developed by beats at time 0. The average amplitude of beat at time 0 was 0.7 cm $H_2O$ and the average rate, 180/min (average weight of crabs, 163 g).

first, although difficult to evaluate, may be dismissed at the gross level on the grounds that whatever tendency for change exists is for an increase in surface area—a direction opposite to that necessary to account for the reduced k. The second may be dismissed on the grounds that, although an increase in volume occurs, and this would tend to reduce the value of k, the extent of the volume change (0.56% body weight in *Libinia* and much less in *Carcinus*) is insufficient to change the volume of the water pool (about 70% body weight) by an amount necessary to account for the reduction. The presence of more than one water compartment can also be considered; although this was not found in preliminary studies in *Libinia,* it has been reported for *Carcinus* (Rudy, 1967). Rudy found that the fast compartment was 60 to 80% of the total volume of exchangeable water; if all of the increase in volume occurred in this compartment, it would not account for the decrease in k.

### *Two possible mechanisms for changes in k*

There is some similarity in the initial change in k in specimens of *Carcinus, Libinia* and *Rithropanopeus* transferred to a dilute salinity. Although this similarity may be superficial, there could be a common mechanism. There are, of course, many possible changes which could account for a reduction in k, but for present purposes, we will consider changes which occur in the unstirred layers at a liquid-solid interface. The concentration of a substance within an unstirred layer may be quite different from its concentration in the free medium, and under some condi-

TABLE II

*Comparison of $P_{osm}$* and $P_d$* for some crabs. References are indicated by superscripts: a, this report; b, Born (1970); c, urine production from Shaw (1961), osmotic gradient from Smith (1970); d, urine production from Binns (1969), osmotic gradient from Smith (1970); e, Rudy (1967); f, Smith (1970).*

| Animal | Medium (% SW) | $P_{osm}^* = L_p^* \frac{RT}{\overline{V}_W} \times 10^4$ [cm³/(g·sec)] | $P_d^* = \frac{kv}{g} \times 10^4$ [cm³/(g·sec)] |
|---|---|---|---|
| *Libinia emarginata* | 100 | $28^a$ | $11^a$ |
| *Pugettia producta* | 100 | $56^a$ | $36^b$ |
| *Carcinus maenas* | 100-94 | | $1.5^a$, $4.6^f$, $3.7^a$ |
| | 80-70 | $5.3^c$, $5.4^d$ | $1.5^e$, $5.3^f$, $2.7^a$ |
| | 50-40 | $4.3^c$, $4.4^d$ | $1.4^e$, $3.9^f$ |
| | 25-35 | $5.1^c$, $7.5^d$ | $3.4^f$ |

tions, the thickness of this zone is an inverse function of the free stream velocity. Unstirred layers have a large influence on the rate of tracer water movement across very permeable membranes, since as permeability increases, diffusion through the unstirred layers becomes rate limiting.

For several crabs (*Rithropanopeus,* Capen, 1972; *Uca,* Hannan and Evans, 1973), it has been shown that 86 to 90% of tracer water exchange occurs in the gill chambers. Thus a change in blood circulation, or external irrigation of the gills could have a major influence on total water exchange. When specimens of *Libinia* were transferred to 80% SW there was a reduction in heart rate (Fig. 2). This could indicate a reduction in the blood circulation in the gills, and might account for the reduction in k. This idea received some support when it was found that water exchange was a function of the perfusion rate in isolated gills of *Libinia* maintained in SW: after 10 min of perfusion at 25, 47, and 90 ml/hr, the concentrations in the perfusion fluid, expressed as a percentage of the external medium, were $6.3 \pm 2.84$ (6), $14.2 \pm 4.56$ (6)*, and $18.2 \pm 10.5$ (5) % $D_2O$ (mean ± SD (N), $* = P < 0.001$, paired *t*-test), respectively.

These is also evidence for a reduction in the rate of irrigation of the gills. In a typical 150-g specimen of *Libinia* in SW, the scaphognathite, or gill bailer, beats 150 to 200 times per minute. When this crab was transferred from 100 to 80% SW, there was a somewhat erratic, but definite reduction in the amplitude of the pressure pulse (Fig. 3), and a small tendency for a reduction in the rate of beat. Furthermore, in some animals, the scaphognathite appeared to stop for periods of several minutes. Most recordings were carried out for a 5-hour period, at which time the scaphognathite beat had not returned to normal. In one 15-hr recording, the scaphognathite beat returned to normal at about 9 hr. Considering the time courses, the change in the amplitude of the scaphognathite beat is better correlated with the change in k than the change in heart rate.

## DISCUSSION

Comparative studies of decapod crustaceans, using tracer water (Rudy, 1967; Thompson, 1970; Hannan and Evans, 1973) and other techniques (Nagel, 1934; Gross, 1957; Herreid, 1969), have shown that there is a relationship between "permeability" and habitat. In general, permeability decreases sequentially in animals from marine, brackish-water, and fresh-water habitats. Among closely related osmoconformers, permeability, as indicated by weight gain, seems to decrease with increasing euryhalinity (Davenport, 1972). *Libinia emarginata* and *Pugettia producta* provide an additional example of this type of relationship, since the lower apparent permeability of *Libinia* (Table II), can be correlated with its great salinity tolerance; *Libinia* can be adapted to 40% SW (Gilles, 1970) while *Pugettia,* to only 50 to 55% SW. These differences between *Libinia* and *Pugettia* are possibly related to the fact that environmental salinity fluctuations are greater on the east coast of the United States, where *Libinia* is found, than on the west coast of the United States, where *Pugettia* is found.

The relationship between tracer water exchange rate (k) and habitat reinforces the belief that k is a meaningful measure of permeability; however, some reservations about the meaning of small changes may be necessary. Generally among decapod crustaceans, changes in salinity have been found to affect k by about 20 to 40%. This change in k is small enough that factors other than permeability could be responsible. One such factor is a change in unstirred layers. In specimens of *Libinia* exposed to a dilute medium, the transient reduction in k, which initially resembles the long-term reduction in *Rithropanopeus harrisii* (Capen, 1972) and *Carcinus maenas* (this report), can be correlated with a reduction in the amplitude of the beat of the scaphognathite. In other studies, there are also indications of reductions in gill irrigation of crabs exposed to a dilute medium (*Libinia* and *Maja verrucosa,* King, 1965; *Carcinus maenas,* Hume and Berlind, 1976). A temporary reduction in gill irrigation could provide a simple mechanism for short-term reductions in k and might confuse the issue of permeability changes since the scaphognathite is not only affected by salinity changes, but oxygen tension (McMahon and Wilkens, 1975) and tidal cycle (Arudpragasam and Naylor, 1964) as well.

Changes in blood flow could also affect k, but the evidence for this is not strong. Reductions in the heart rates of *Libinia* and *Carcinus* were thought by Cornell (1973, 1974) to provide a possible explanation for reductions in k; however, further data make this possibility less likely. In addition, Hume and Berlind (1976) found that the heart rate in *Carcinus* increases in dilute media. The cause of this discrepancy between the results of Hume and Berlind and my own is not known.

It is generally believed that the effects of unstirred layers can be much greater on estimates of diffusive water permeability ($P_d$) than on osmotic water permeability ($P_{osm}$) (House, 1974). However, much of the discrepancy between these estimates may be eliminated by adequate stirring (Dainty and House, 1966). Thus, one possible way of evaluating the effects of unstirred layers comes from the comparison of $P_{osm}$ and $P_d$.

It should be pointed out that it is difficult to justify the necessary assumptions in comparing $P_{osm}$ and $P_d$ in something as "simple" as an isolated sheet of epithelium, let alone an intact animal. But, we are guided by the words of House (1974, p. 341): "In view of the dubieties about errors in $P_d$ and $L_p$ values one has no proper right to compare them. Nevertheless, I shall do so." Table II shows $P_{osm}$* and $P_d$* for *Carcinus, Libinia* and *Pugettia.* In *Libinia* and *Pugettia,* $P_{osm}$* was determined from the rate of weight gain in 80% SW at time 0 and the osmotic gradient caused by the transfer from 100% SW. In *Carcinus,* $P_{osm}*$ was determined from published values of urine production rates, and osmotic gradients, for animals in a steady state in dilute SW. For estimates of $P_d*$, it was assumed that the exchangeable water in all crabs was 70% body weight. $P_{osm}*/P_d*$ is greater than unity in all cases. Interpreting these results is a matter for speculation, but I suggest that these data are consistent with the possibility that changes in unstirred layers could have a major influence on water exchange rates in all of these crabs since the ratio of $P_{osm}*/P_d*$ does not differ greatly among *Carcinus, Libinia* and *Pugettia.*

Thus, a transient increase in the thickness of unstirred layers surrounding the gill might explain the transient reduction in k in a crab such as *Libinia.* Such a mechanism could also affect the initial phases of a long-term reduction in k in a crab such as *Carcinus,* but the evidence suggests that the maintenance of long-term reductions in k are the result of some other mechanism, which may be under hormonal control (see Tullis and Kamemoto, 1974, and Berlind and Kamemoto, 1977). The existence of this other mechanism is demonstrated by the fact that the isolated gills of *Callinectes spadius* and *Cancer irroratus* from crabs adapted to 40% SW have a lower water exchange rate than do those from crabs adapted to 100% SW (Cantelmo, 1977).

In the strictest sense, it is possible to state that a change in water permeability has not been demonstrated beyond doubt in any decapod crustacean. But regardless, a process that can reduce the effect of an osmotic gradient is potentially of adaptive value. Thus, we should ask if a reduction in k reflects the action of such a process. A definitive answer to this question is not yet available for *Libinia, Pugettia,* and many other decapod crustaceans.

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## SUMMARY

1. Estimates of osmotic water permeability suggest that *Libinia emarginata* [166 μl/(g·hr·osmol)] is less permeable to water than *Pugettia producta* [338 μl/(g·hr·osmol)]. Data on tracer water exchange supports this conclusion and the differences in apparent permeability can be correlated with differences in habitat.

2. Short-term changes in $D_2O$ water exchange were examined in specimens of *Carcinus maenas* and *Libinia emarginata.* When these crabs were transferred from 100 to 80% sea water, there was an initial reduction in k in (1/hr), the

hourly water exchange fraction, of from 1.9 to 1.4 and from 5.8 to 4.3 in *Carcinus* and *Libinia,* respectively. In both crabs, the initial response to the dilute medium is similar; however, in *Libinia,* the reduction in k is transient while in *Carcinus* it is a long-term response.

3. Estimates of osmotic ($P_{osm}$*) and diffusive ($P_d$*) water permeabilities for *Carcinus, Libinia* and *Pugettia* indicate that the ratio of $P_{osm}*/P_d*$ is about 2, which suggests that unstirred layers could have a major influence on tracer water movement in all of these crabs. It is proposed that the initial changes in k, which occur during adaptation to a dilute medium, are at least partly the result of an increase in thickness of the unstirred layers surrounding the gills, caused by a reduction in the flow of medium through the gill chamber.

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